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Sarcopterygians from the Lochkovian (Lower Devonian) of Nanning, Guangxi, China

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Abstract Here we report a left cheek plate of *Psarolepis*, a postparietal shield of *Youngolepis*, a skull of *Diabolepis*, and a scale of *Styloichthys* from the Lianhuashan and Nahkaoling formations (Lochkovian, Lower Devonian) of Nanning, Guangxi. This marks the first report of *Diabolepis* and *Styloichthys* beside Qujing, Yunnan, and the latest occurrence of *Psarolepis* to date. The fossil community displays significant similarities to the Xujiachong Assemblage, and provides new data for the Lower Devonian stratigraphic correlation between southwestern China and northern Vietnam. Given the latest dating constraint based on the conodont evidence, we regard that the Xujiachong Assemblage has a much longer range than previously supposed, extending from the latest Lochkovian to the end of Pragian. We propose that the transition of the Nahkaoling and Lianhuashan formations in Nanning might correspond to the Guijiatun Formation in Qujing. The relatively large size of fish individuals from Guangxi is probably attributed to the increase in the oxygen content of the ocean.

Key words Nanning, Guangxi; Lochkovian, Lower Devonian; Xujiachong Assemblage, Lianhuashan Formation, Nahkaoling Formation; Sarcopterygians

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1 Introduction

Early sarcopterygian fossils from the late Silurian to Lochkovian (Early Devonian) interval are abundant in eastern Yunnan, southwestern China. They are represented by the stem sarcopterygians (e.g., *Psarolepis*, *Achoania*, *Guiyu*, and *Sparalepis*) and the crown sarcopterygians (e.g., *Youngolepis*, *Diabolepis*, and *Styloichthys*) (Chang and Yu, 1981; 1984;

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Zhu et al., 1999, 2001, 2009; Zhu and Yu, 2002; Choo et al., 2017; Cui et al., 2023), many of which have greatly reduced the morphological disparities between the earliest representatives of major gnathostome clades and provided important insights into the origin and early evolution of sarcopterygians. However, these sarcopterygian genera have never been reported from other sites except for *Psarolepis* and *Youngolepis* from northern Vietnam (Tông-Dzuy et al., 1997). Here, we report a left cheek plate of *Psarolepis*, a postparietal shield of *Youngolepis*, a skull of *Diabolepis*, and a scale of *Styloichthys* from the Lochkovian of Nanning, Guangxi. These sarcopterygians from Guangxi are very suggestive of the Xitun Fauna in Qujing, Yunnan (Zhao and Zhu, 2010).

The fossil locality is in the suburbs of Nanning (Fig. 1), where the Lower Devonian is widely distributed and exposed. The Lower Devonian in Nanning includes the Lianhuashan, Nahkaoling, Yukiang, Moding formations and the lower part of the Najiao Formation in ascending order. The stratigraphic succession was described and mapped comprehensively by previous researchers (Kuang et al., 1989; Zhong et al., 1992).

The Lianhuashan Formation rests unconformably on the Cambrian rocks (Kuang et al., 1989). Based on lithology, it can be divided into three members: the Lingli Member, which is dominated by quartz sandstone; the Hengxian Member, which is characterized by dolostone intercalations; the Liukankou Member, which is characterized by the common occurrence of calcareous materials in siltstone (Kuang et al., 1989) (Fig. 1B). Invertebrate fossils were yielded from the Lianhuashan Formation, mainly bivalves and ostracods, most of which are endemic species. The lower part of the Lianhuashan Formation yielded fossil fish including the antiarchs *Yunnanolepis chii* (P'an et al., 1978; Liu, 1992), *Zhanjilepis* sp. (Liu, 1992), and the arthrodires *Asiacanthus kaoi* and *A. suni* (P'an, 1964), which are also known from the Xitun and Xishancun formations in eastern Yunnan (Liu, 1992). The top part of the Lianhuashan Formation yielded the arthrodire *Parawilliamsaspis yujiangensis* (Liu, 1980), the antiarch *Chuchinolepis gracilis* (P'an and Wang, 1978; P'an et al., 1978; Liu, 1992), and the galeaspids *Eugaleaspis lianhuashanensis* (Liu, 1986), *Polybranchiaspis*, and *Sanchaspis* (Gai et al., 2022).

The Nahkaoling Formation is dominated by fine sandstone, siltstone, and mudstone. It can be divided into the Gaoling Member and the Mahuangling Member. The bottom of the Gaoling Member yielded the vertebrate macro-remains including the galeaspids *Nanningaspis zengi* (Gai et al., 2018), *Asiaspis liangi*, *Huananaspis cupido* (Zhang et al., 2023), *Gantarostrataspis*, *Rhegmaspis*, *Wumengshanaspis*, *Sinoszechuanaspis*, *Qingmenaspis*, *Lungmenshanaspis*, *Wenshanaspis*, and *Dongfangaspis* (Gai et al., 2022), and the arthrodires *Szelepis* sp. (Liu, 1982), *Asiacanthus multituberculatus* (Liu, 1982) and *Yujiangolepis liujingensis* (Wang et al., 1998; Zhu et al., 2000; Dupret et al., 2009). Most of the materials described in this paper are uncovered from this layer. Here, we regard the age of this layer as the latest Lochkovian, in view of the dating constraint based on the recent conodont evidence from central Guangxi (Lu et al., 2023).

Other fish macro-fossils recovered from Nanning area include the arthrodire *Buchanosteus guangxiensis* (Wang, 2005), the galeaspids *Asiaspis expansa* (P'an et al., 1975), and *Antiquisagittaspis cornuta* (Liu, 1985) from the upper part of the Nahkaoling Formation, and the lungfish *Cathlorhynchus zengi* from the Yukiang Formation (Qiao and Zhu, 2015).

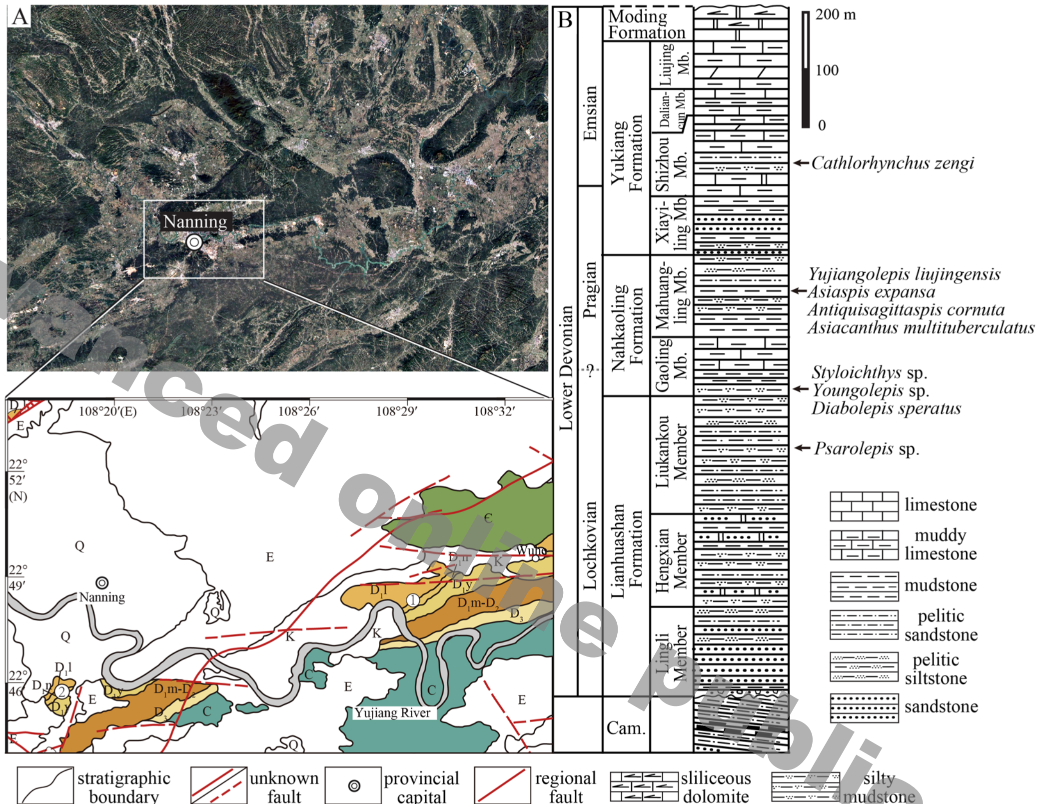

Fig. 1 Locality and geological setting of the fossil sites

A. location and geologic map of the fossil locality (based on the open geological data in the National Geological Archives of China:http://www.ngac.org.cn/Map); B. stratigraphic sequence of the Lower Devonian in the Nanning-Liujing district (modified after Kuang et al., 1989; Lu et al., 2023)

① Xianhu (22°48'50"N; 108°28'55"E); ② Wuxiangling (22°45'49"N; 108°17'52"E); Є. Cambrian; D_1l. Lianhuashan Formation; D_1n. Nahkaoling Formation; D_1y. Yukiang Formation; D_1m-D_2. Lower Devonian Moding Formation and the Middle Devonian; D_3. Upper Devonian; C. Carboniferous; K. Cretaceous; E. Paleogene; Q. Quaternary

2 Materials and methods

This study involves the cheek plate of *Psarolepis* (IVPP V20340) from the middle part of the Lianhuashan Formation, and a skull of *Diabolepis* (V33254), a postparietal shield of *Youngolepis* (V33255), and a scale of *Styloichthys* (V33256) from the Nahkaoling Formation (Lochkovian) of Nanning, Guangxi. All specimens were prepared mechanically using a needle and are permanently housed for reference in the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences (IVPP).

The skull of *Diabolepis* (IVPP V33254) and the scale of *Styloichthys* (V33256) were scanned at IVPP, using the GE Phoenix v|tome|x m300&180 micro-computed tomography scanner. The specimens were scanned with a beam energy of 180 kV and a flux of 100 mA at a detector resolution of 7.4 μm per pixel (V33254) and 5.3 μm per pixel (V33256), using a 1440° rotation with a step size of 0.25° and an unfiltered aluminum reflection target. 1440 transmission images were reconstructed in a 2048 × 2048 matrix of 1536 slices. Scan data was analyzed using Mimics v.25.0 (http://biomedical.materialise.com/mimics; Materialize).

3 Systematic paleontology

Osteichthyes Huxley, 1880

Sarcopterygii Romer, 1955

***Psarolepis* Yu, 1998**

***Psarolepis* sp.**

(Figs. 2, 3)

Referred specimen IVPP V20340, a left cheek plate with maxillary and preopercular.

Locality and horizon Xianhu (22°48'50"N; 108°28'55"E), the suburb of Nanning, Guangxi, China; Lianhuashan Formation, Lochkovian, Lower Devonian.

Description The material IVPP V20340 is a left cheek plate with maxillary and preopercular bones. It measures about 4.0 cm in total length and 1.6 cm in height. The erosion during preservation makes detecting the ornamentation on the external surface impossible. Still, the ornamentation on the external surface hints at a possible preopercular canal (pc, Fig. 2) running along the dorsal margin. Consistent with *Psarolepis* from Qujing (IVPP V11255, V11256.2; Zhu et al., 1999), actinopterygians (Fig. 3A), and *Guiyu* (Fig. 3D), the preopercular (Pop, Fig. 2) lacks a jugal canal that runs horizontally to connect the infraorbital canal as in other sarcopterygians (Fig. 3B, C). The preopercular measures longer than the total length of the maxillary in V20340, whereas in V11256.2, the preopercular is approximately as long as the maxillary (Fig. 3E). The dorsal portion of the preopercular carries three large foramina (fo1–3, Fig. 2) as to V11256.2, like those found in the dermal cheeks of *Youngolepis* and *Kenichthys* (Chang and Zhu, 1993; Zhu and Ahlberg, 2004), as well as in the lower jaws of *Psarolepis*, *Youngolepis*, *Powichthys*, and some porolepiforms (Jarvik, 1980). However, the large pores are not led by the grooves as in *Youngolepis* (Chang, 1991). The maxillary (Mx, Fig. 2) is elongated triangular and about six times as long as deep. The ventral margin of the Nanning specimen is not as convex as in V11256.2 (Fig. 3E). There is a row of marginal teeth along the ventral border of the bone, mostly distributed along the mesial portion. There is no trace of teeth on the anterior part of the maxillary, due to poor preservation. There is a broad contact between the maxillary and the preopercular, leaving only about 1/3 of the total length to accommodate the jugal as in *Guiyu* (Gai et al., 2017; Qiao and Zhu, 2010). Groups of pores

(grp, Fig. 2) can be seen along the anterior portion of the cheek plate as in V11256.2. These groups of small pores can also be found in osteolepiforms (Jarvik, 1966), *Powichthys* (Jessen, 1975, 1980), *Porolepis* (Jessen, 1975) and *Youngolepis* (Chang, 1991).

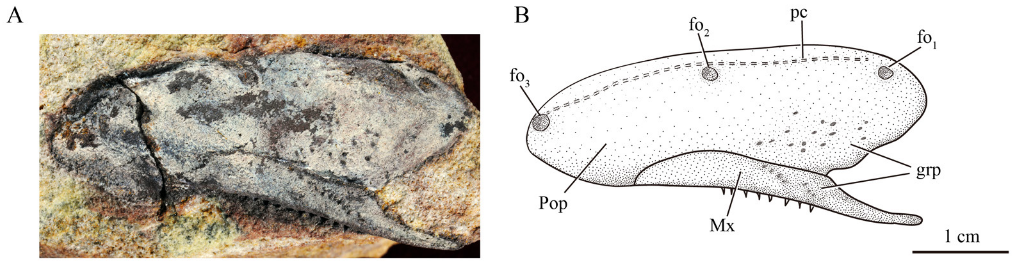

Fig. 2 Photograph (A) and interpretative drawing (B) of *Psarolepis* sp. (IVPP V20340)
Abbreviations: fo_1-fo_3. foramina; grp. groups of pores; Mx. maxillary;
pc. preopercular canal; Pop. preopercular

Remarks and comparison *Psarolepis romeri* is one of the earliest osteichthyans known so far. It was recovered from the late Silurian–Early Devonian of Yunnan, southwestern China, and northern Vietnam (Tông-Dzuy et al., 1997; Yu, 1998; Zhu et al., 1999; Zhu and Schultze, 2001). Materials assignable to this genus include the skulls, lower jaws, cheek bones, shoulder girdles, scales, and fin spines (Yu, 1998; Zhu et al., 1999; Zhu and Schultze, 2001; Qu et al., 2013).

Psarolepis was initially described as a possible member of Dipnomorpha by Ahlberg (1991). In the recent phylogenetic analyses (Zhu et al., 1999, 2006, 2009, 2013, 2016; Basden et al., 2000; Zhu and Schultze, 2001; Zhu and Yu, 2002; Davis et al., 2012; Giles et al., 2015; Lu et al., 2016; Qiao et al., 2016; Choo et al., 2017), *Psarolepis* is assigned to the psarolepids (Choo et al., 2017), a cluster also comprising *Guiyu*, *Achoania*, and *Sparalepis* (Lu et al., 2017). This clade manifests a combination of features found in both sarcopterygians and actinopterygians (e.g. pectoral girdle structures, the cheek and operculo-gular bone pattern, and scale articulation) (Zhu et al., 1999; 2009). They also reveal a combination of osteichthyan and non-osteichthyan features, including spine-bearing pectoral girdles and spine-bearing median dorsal plates found in non-osteichthyan gnathostomes, as well as cranial morphology and derived macromeric squamation found in crown osteichthyans (Zhu et al., 2009). They were referred to as stem sarcopterygians in some earlier studies (Basden et al., 2000; Zhu et al., 2009; Friedman and Brazeau, 2010). Besides the affinity with early sarcopterygians, *Psarolepis* has also been assigned as a stem osteichthyan when it was first placed in the phylogenetic analysis (Zhu et al., 1999). Qu et al. (2015) reported the absence of tooth enamel in *Psarolepis*, contrasting with its presence in both actinopterygians and sarcopterygians. This character distribution corroborates *Psarolepis* as a stem osteichthyan. The discovery of *Ptyctolepis* reassessed psarolepids as stem osteichthyans (Lu et al., 2017).

IVPP V20340 is consistent with the previously reported V11255 and V11256.2 (Zhu

et al., 1999) in the presence of a complete preopercular canal, three large foramina on the preopercular, the lack of a jugal canal, the absence of a separate squamosal and the groups of pores along the anterior portion of the cheek plate. These characters distinguish them from all other sarcopterygians. Nevertheless, there is no trace of a short vertical canal running from the midpoint of the preopercular canal as in V11256.2 (Zhu et al., 1999).

The anterior margin of the preopercular of *Psarolepis* is curved rather than straight in *Guiyu*. The sensory canal on the preopercular is along the dorsal margin and shows the path of the preopercular canal as in chondrichthyans, acanthodians, and actinopterygians (Fig. 3A), which is at odds with the condition in other sarcopterygians. The separate squamosal, which always carries the jugal canal, is absent in psarolepids and actinopterygians (Fig. 3A). In crown sarcopterygians, the preopercular canal always has a horizontal portion (the jugal canal) extending forward to join the infraorbital canal within the jugal bone (Forey, 1998). The posteriorly expanded maxillary in broad contact with the preopercular is consistent with the condition in actinopterygians, and onychodont sarcopterygians (Long, 2001).

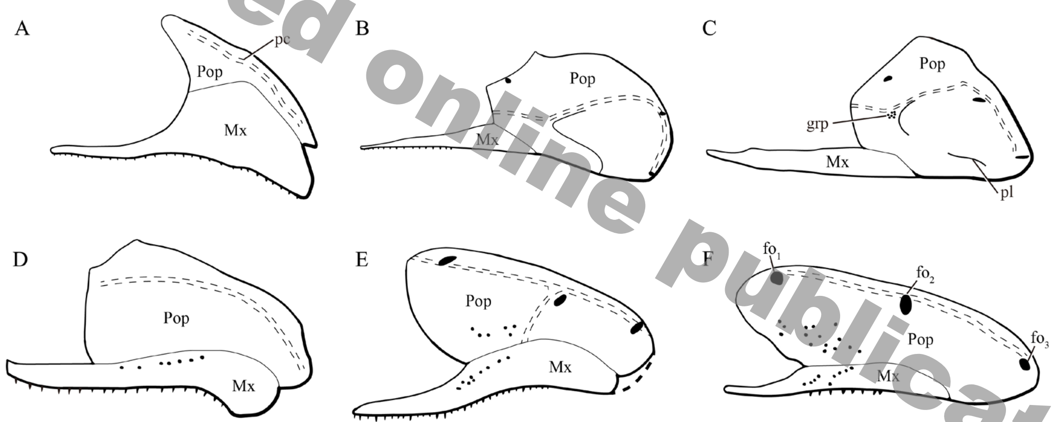

Fig. 3 Comparison of osteichthyans cheek plates
A. *Mimipiscis toombsi* (modified from Choo, 2012); B. *Kenichthys campbelli* (modified from Zhu and Ahlberg, 2004); C. *Youngolepis* sp. (modified from Chang, 1991; Cui et al., 2022);
D. *Guiyu oneiros* (modified from Zhu et al., 2009); E. *Psarolepis romeri* (modified from Zhu et al., 1999);
F. *Psarolepis* sp. (IVPP V20340)
Abbreviations: fo_1–fo_3. foramina; grp. groups of pores; Mx. maxillary; pc. preopercular canal; pl. pit-line; Pop. preopercular

Styloichthys Zhu & Yu, 2002

Styloichthys sp.

(Fig. 4)

Referred specimen IVPP V33256, a flank scale.

Locality and horizon Wuxiangling (22°45'49"N; 108°17'52"E), Nanning, Guangxi, China; Nahkaoling Formation, Lochkovian, Lower Devonian.

Description An incomplete right flank scale is preserved, lacking the ventral part (Fig. 4). It is 14.5 mm long, and 18.0 mm high. In crown view, the anterior and posterior edges (e.a, e.p, Fig. 4B, C) are straight and parallel. The cosmine-covered free field bears fourteen longitudinal ridges (r, Fig. 4B, C), with pores (po, Fig. 4B, C) lying between the ridges. The free field's dorsal edge (e.d, Fig. 4B, C) is curving. The depressing field (f.d, Fig. 4B, C) is very narrow. The peg (p, Fig. 4B, C) has a broad base. The dorsal part of the peg is missing, presumably forming an apex. The anterodorsal process is not preserved. The base of the scale is buried in the matrix.

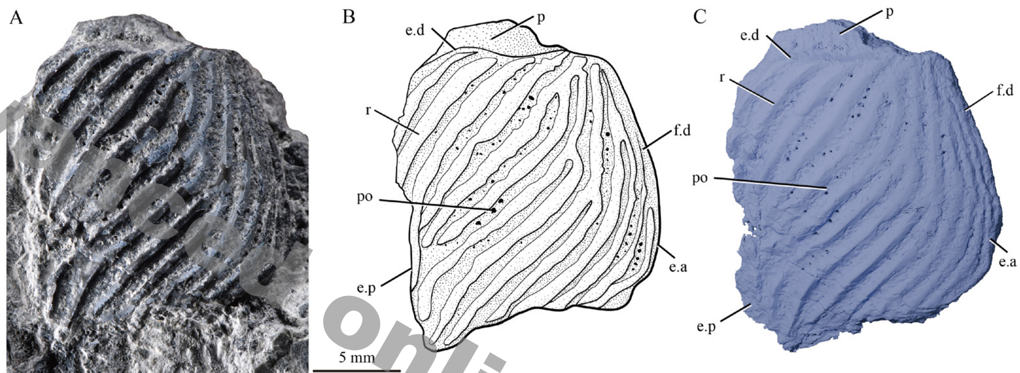

Fig. 4 Photograph (A), interpretative drawing (B), and 3D virtual model (C) of the scale of *Styloichthys* sp. (IVPP V33256)
Abbreviations: e.a. anterior edge; e.d. dorsal edge; e.p. posterior edge; f.d. depressed field; p. peg; po. pores; r. ridges

Remarks and comparison The genus *Styloichthys* from the Xitun Formation was established by Zhu and Yu (2002), initially regarded as the sister group of rhipidistians, while Friedman (2007) considered *Styloichthys* as the most basal coelacanth. Many follow-up studies (Zhu and Yu, 2004; Zhu et al., 2006; Lu and Zhu, 2008; Cui et al., 2023, in press) corroborated the former. The rhombic scales in *Styloichthys* are characterized by relatively large pores and parallel ridges, showing a transition from stem sarcopterygians to crown sarcopterygians (Cui et al., in press). Morphologically, IVPP V33256 is most like the Morphotype 4 scales in the prominent peg and absent anteroventral process described by Cui et al. (in press). However, V33256 is significantly larger than those from the Xitun and Guijiatun formations.

Styloichthys has a cosmine surface with relatively large pores between ridges on the dermal bones and scales. Contrasting with the materials from the Xitun and Guijiatun formations (Cui et al., in press), the material in Guangxi is remarkably larger. It seems to be a proportionate enlargement as the number of ridges and pores resembles the materials from the Xitun Formation. The larger scale suggests a larger body of *Styloichthys* in Guangxi during the Early Devonian.

Dipnomorpha Ahlberg, 1991

***Youngolepis* Chang & Yu 1981**

***Youngolepis* sp.**

(Fig. 5)

Referred specimen IVPP V33255, a postparietal shield.

Locality and horizon Wuxiangling (22°45'49"N; 108°17'52"E), Nanning, Guangxi, China; Nahkaoling Formation, Lochkovian, Lower Devonian.

Description The postparietal shield is almost complete, only lacking the anterior-right part (Fig. 5A, B). It is relatively larger than the previously reported ones, about 11.0 cm in maximum width and 9.0 cm in length (Fig. 5A). All bones of the postparietal shield are covered by cosmine. Groups of small pores (grp, Fig. 5B) can be found along the supratemporal series indicating the pathway of the otic sensory canal. Some large pores are scattered along the lateral portion of the right postparietal. The transverse suture between the parietals and the postparietals is always blocked by one of the elements of the longitudinal supratemporal series, however, the natural suture cannot be traceable as the ledge is broken. The sutures in IVPP V33255 are well preserved, including those between the marginal bones and postparietal, as well as between the two postparietals. The paired postparietals have the length more than 2.5 times the width, and meet each other along a slightly curved median suture. The posteriorly protruding angle is present in the posterior margin of the postparietal as in other specimens of *Youngolepis* and most dipnoans, e.g., *Diabolepis* (Chang, 1995), *Dipterus* (White, 1965), *Arquatichthys* (Lu and Zhu, 2019), and *Chirodipterus* (Miles, 1977). Two pairs of marginal bones are present alongside the postparietals. The posterior marginal bone, referred to as the tabular (Ta, Fig. 5B), has a lateral wing projection, marking the maximum width of the postparietal shield. The tabular occupies about half the length of the whole postparietal shield. The supratemporal (St, Fig. 5B) has a similar overall shape as in IVPP V6553 (Fig. 5C), whereas the anterior edge is not traceable. The middle and posterior pit-lines (mpl, ppl, Fig. 5A, B) are present on the postparietals. The middle pit line is much longer than the posterior pit-line and reaches the suture between the postparietal and tabular as in V6183 (Fig. 5D; Chang, 1982). No tabular pit-line can be seen.

Remarks and comparison *Youngolepis* was named by Chang and Yu (1981) based on a parietal shield of the type species *Y. praecursor*. It has been reported from the base of Xishancun, Xitun, and Guijiatun formations of Yunnan (Chang and Yu, 1981; Chang, 1982, 1991; Kuang et al., 1989; Zhu et al., 1994; Zhu and Fan, 1995; Cui et al., 2022), the base of Bac Bun Formation, the top of Si Ka Formation of Bac Bo, and lower part of Khao Lock Formation of Tong Vai, northern Vietnam (Tông-Dzuy and Janvier, 1994). Recent analyses placed *Youngolepis* within Dipnomorpha at the base of the lungfish lineage (Cui et al., 2022, in press). It is a pivotal taxon for studying the specialized character acquisition of lungfish.

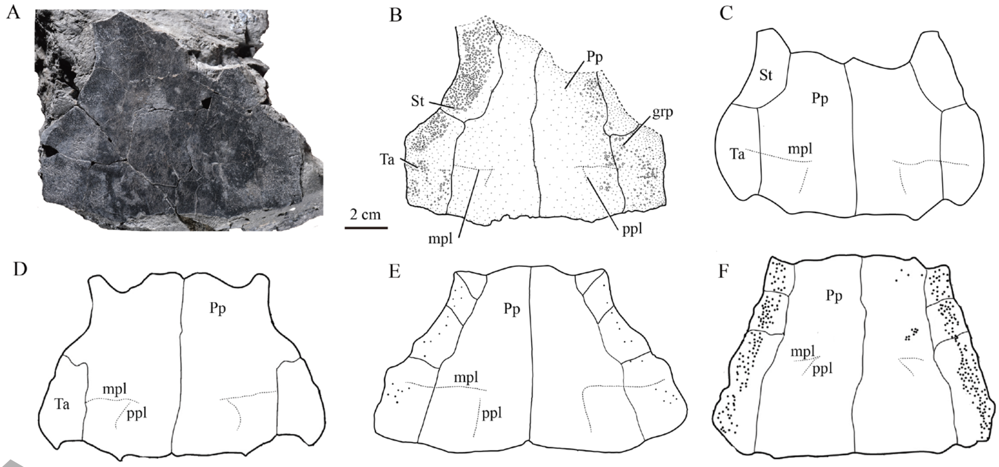

Fig. 5 Photograph and comparison of postparietal shields in dipnomorphs
A–B. *Youngolepis* sp. (IVPP V33255): A. photograph, B. reconstruction; C–D. *Y. praecursor*: C. V6553, D. V6183 (modified from Chang, 1982); E. *Powichthys thorsteinssoni* (modified from Jessen, 1975); F. *Arquatichthys porosus* (modified from Lu and Zhu, 2019)
Abbreviations: grp. groups of pores; mpl, middle pit-line; ppl. posterior pit-line; Pp. postparietal; St. supratemporal; Ta. tabular

As noticed by Chang (1982), the elements of the postparietal shield have fused with each other in various ways. Thus, not all sutures can be traced in the available specimens. Of all reported specimens, the Nanning material (IVPP V33255) shows an outline of the postparietal shield most like the previously described specimen V6553 (Fig. 5C). Both specimens share the paired posteriorly projecting processes, two pairs of marginal bones, and the posteriorly situated middle and posterior pit-lines. In some specimens of *Youngolepis*, only one pair of marginal bones can be seen on the postparietal (Fig. 5D). In the primitive dipnomorphs *Powichthys* (Fig. 5E) and *Arquatichthys* (Fig. 5F), there are at least three pairs of marginal bones. The middle pit-line of the Nanning specimen does not extend to the tabular, which resembles the condition in V6183 (Fig. 5D; Chang, 1982) and *Arquatichthys* (Fig. 5F; Lu and Zhu, 2019). The middle and posterior pit-lines are situated posteriorly in the postparietal shield, which is suggestive of *Powichthys*, *Osteolepis*, *Eusthenopteron* (Jarvik, 1980), and other materials of *Youngolepis*, contrasting the condition in *Arquatichthys* (Fig. 5F). Besides, V33255 shows the total length of 9 cm. Considering the ratio of the parietal and postparietal shields is about 1.5–1.9, the total length of the cranial shield of the Nanning specimen is estimated at about 25 cm, much larger than other specimens. The total length of the *Youngolepis* skull from the Xitun Fauna ranges between 2 to 10 cm.

Order Dipnoi Müller, 1845

***Diabolepis* Chang & Yu, 1984**

***Diabolepis* speratus Chang & Yu, 1984**

(Fig. 6)

Referred specimen IVPP V33254, a complete skull roof.

Locality and horizon Wuxiangling (22°45'49"N; 108°17'52"E), Nanning, Guangxi, China; Nahkaoling Formation, Lochkovian, Lower Devonian.

Description The new material is a complete skull roof, which measures about 2.5 cm in maximum length and 2.0 cm in width. The ratio between the length and the width is about 1.25. There is no pineal opening on the skull roof, but a corresponding elevation is present as in the holotype of *Diabolepis* and other dipnomorphs such as *Younglolepis* and *Chirodipterus liangchengi* from China (Song and Chang, 1991). Based on the CT scanning data, a posteriorly directed pineal canal (c.pi, Fig. 6D) rising from the endocast disappears under the elevation. The cosmine-covered skull has no traceable sutures to indicate the bone boundaries in the anterior portion. Three oblique pores (soc.p, Fig. 6B, E) are visible around the anterolateral elevation profile, showing the path of the right supraorbital sensory canal (soc, Fig. 6C, D). The CT scanning data also reveals the sensory canal sending out its branching tubes, which open in pores on the skull roof. The paired supraorbital sensory canals converge along the mesial edge of the nasal cavity. The nasal cavity (nc, Fig. 6D) is transversely subtriangle-shaped, as in *Youngolepis* (Chang, 1982). The I-bones posteriorly meet each other in midline while the anterior parts of both I-bones are separated by B-bone or a median element and carry pit-lines corresponding to the middle and posterior pit-lines (Fig. 6B). The anteromesial margins of paired I-bones form a V-shaped border to accommodate B-bone (Fig. 6B). On the right lateral view, the orbit diameter is about 15% of the skull roof (Fig. 6E).

Remarks and comparison *Diabolepis speratus* was regarded as the sister group of all typical lungfish. Two complete skull roofs have been reported previously, IVPP V7237 (an adult specimen) and V7238 (a juvenile specimen) (Chang and Yu, 1984; Chang, 1995). *Diabolepis* is characterized by the dermal skull roof with anterior portion relatively long; I-bones anteriorly separated from each other by a median element or B-bone but posteriorly meeting each other in midline; snout fairly short and orbit anteriorly positioned; no pineal opening but with the pineal elevation; the posterior process of I-bone and the nasal capsules at mouth margin.

Of the two previously reported specimens, the Nanning specimen shows more similarities to V7237 (an adult individual) in the comparable size, the ratio between the length and the width (about 1.2), the ratio of maximum width to the total length (80% and 83% respectively) and the much smaller orbit (with their diameter about 15% of the skull length). The juvenile individual V7238 is much smaller with the total skull about half as long as those of V7237 and V33254. Its ratio of maximum width to the total length is 67% and the orbit diameter is about 25% of the skull length, showing that the orbit is larger in juvenile fishes than adults (Chang, 1995). As in the two previously reported skulls, V33254 bears the posterior process of I-bone, the pineal elevation; I-bones meet each other in the midline of skull roof. However, the new specimen has an anterior cosmine-covered skull without bone sutures and no traceable Westoll-lines on the skull.

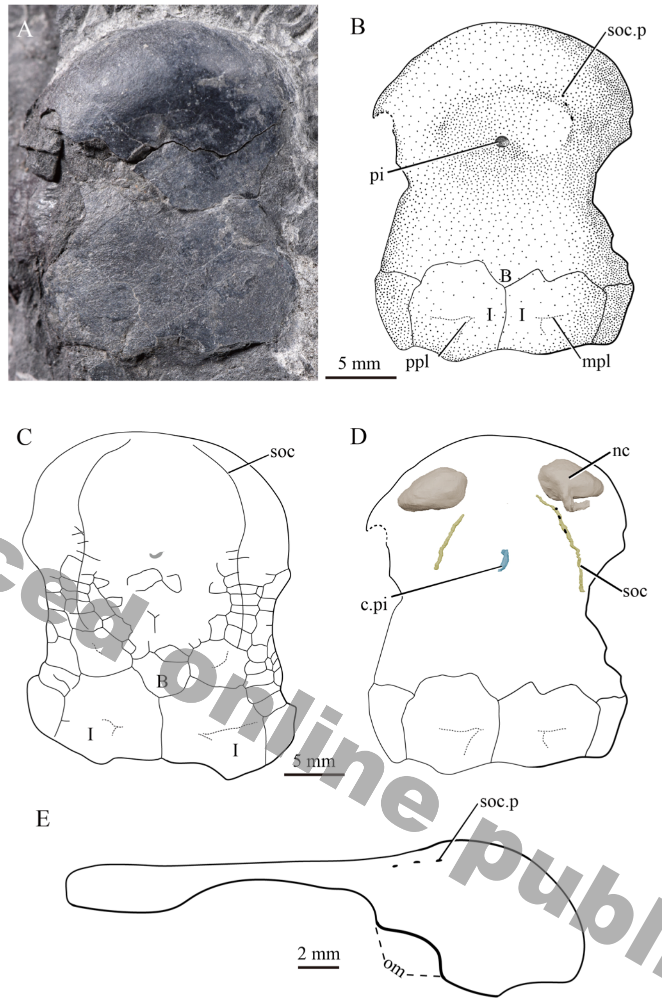

Fig. 6 Photograph and reconstructions of skull roofs and endocast of *Diabolepis speratus*
A, B, D, E. IVPP V33254: A. photograph, B. interpretive drawing, D. 3D virtual model of recognizable structures of the endocast, E. interpretive drawing in lateral view;
C. interpretive drawing of IVPP V7237 (modified from Chang and Yu, 1984)
Abbreviations: c.pi. pineal canal; mpl. middle pit-line; nc. nasal capsule; om. orbital margin; pi. pineal; ppl. posterior pit-line; soc. supraorbital canal; soc.p. pores for supraorbital canal

4 Discussion

The four forms of sarcopterygians from the Lower Devonian of Guangxi expand their distributions in the South China Block. *Psarolepis* was recovered from the late Silurian–Early Devonian of Yunnan, southwestern China, and northern Vietnam (Tông-Dzuy et al., 1997; Yu, 1998; Zhu et al., 1999; Zhu and Schultze, 2001). Most *Psarolepis* specimens from Yunnan derive from four beds at the same locality in Qujing, the first bed being in the Yulungssu Formation (Pridoli), the second and third beds in the Xishancun Formation (early Lochkovian), and the fourth bed in the Xitun Formation (mid-late Lochkovian) (Zhao and Zhu, 2010).

Youngolepis was found from the base of Xishancun, Xitun, and Guijiatun formations of Yunnan (Chang and Yu, 1981; Chang, 1982, 1991; Kuang et al., 1989; Zhu et al., 1994; Zhu and Fan, 1995), the base of Bac Bun Formation, the top of Si Ka Formation of Bac Bo, and lower part of Khao Lock Formation of Tong Vai, northern Vietnam (Tông-Dzuy and Janvier, 1994). *Styloichthys* and *Diabolepis*, to date, are only otherwise known from the Xitun Formation of Qujing. The Xitun Formation consists mainly of greyish-blue and purple calciferous mudstones, which yield abundant bivalves, fish, and rare fragmentary plants.

The transition of the Nahkaoling and Lianhuashan formations in Nanning was correlated to the galeaspid *Sanqiaspis*-bearing beds, i.e., Xujiachong Formation in Qujing and Posongchong Formation in Zhaotong and Wenshan, Yunnan (Gai et al., 2022). The fish community from these beds is assigned to the *Sanchaspis-Asiaspis* assemblage (vertebrate assemblage III) (Zhu et al., 2000) or the Xujiachong Assemblage (Zhao and Zhu, 2010). This assemblage is assumed to be characterized by the radiation of Eugaleaspidiformes and Huananaspidiformes (Zhao and Zhu, 2010), along with some other galeaspid representatives with a pronounced rostral process, such as the polybranchiaspids *Gumuaspis* and *Nanningaspis* (Wang and Wang, 1992; Gai et al., 2018; 2022). Sarcopterygians in the Xujiachong Assemblage include Onychodontidae indet., *Arquatichthys*, *Qingmenodus*, *Tungsenia*, and *Euporosteus* from Zhaotong, Yunnan (Lu and Zhu, 2008, 2019; Lu et al., 2012, 2016).

Tông-Dzuy and Janvier (1994) and Tông-Dzuy et al. (2013) thought that the Devonian deposits of the East Bac Bo Zone are strikingly similar to those of Guangxi (South China), i.e. the Si Ka, Bac Bun, and Mia Le formations of the Bac Bo Region correspond to the Lianhuashan, Nahkaoling, and Yukiang formations of Guangxi. The transition layers of Si Ka and Bac Bun formations have yielded *Youngolepis* (Tông-Dzuy and Janvier, 1990, 1994) and an indeterminate lungfish (Tông-Dzuy and Janvier, 1994; Tông-Dzuy et al., 2013). These beds have also been regarded as the Xujiachong Assemblage (Gai et al., 2022).

The Xujiachong, Posongchong and the top of Si Ka formations, which comprise *Sanqiaspis*-bearing beds, were assigned to Pragian previously based on comprehensive analyses of stratigraphic sequences and fossil assemblages (Ma et al., 2009; Zhao and Zhu, 2010; Qie et al., 2019; Gai et al., 2022). However, the conodonts *Amydrotaxis praejohnsoni* and *Eognathodus* cf. *E. irregularis* have recently been reported from the base of the Nahkaoling Formation in central Guangxi (Lu et al., 2023). This infers the lower boundary of the Nahkaoling Formation, is dated more accurately to be approximately the middle Lochkovian or even much older (Lu et al., 2023). As such, we regard that the age of the Xujiachong Assemblage at the Liujing Section can be traced back as early as the latest Lochkovian, that is, older than its occurrences at the Qujing and Zhaotong sections. It demonstrates that the Xujiachong Assemblage has a much longer range than previously supposed, extending from the latest Lochkovian to the end of Pragian. Correspondingly, we propose that the transition

of the Nahkaoling and Lianhuashan formations in Nanning might correspond to the Guijiatun Formation in Qujing (Fig. 7). However, more precise temporal calibration of the Xujiachong Assemblage relies on detailed investigations of the biostratigraphy in South China in the future.

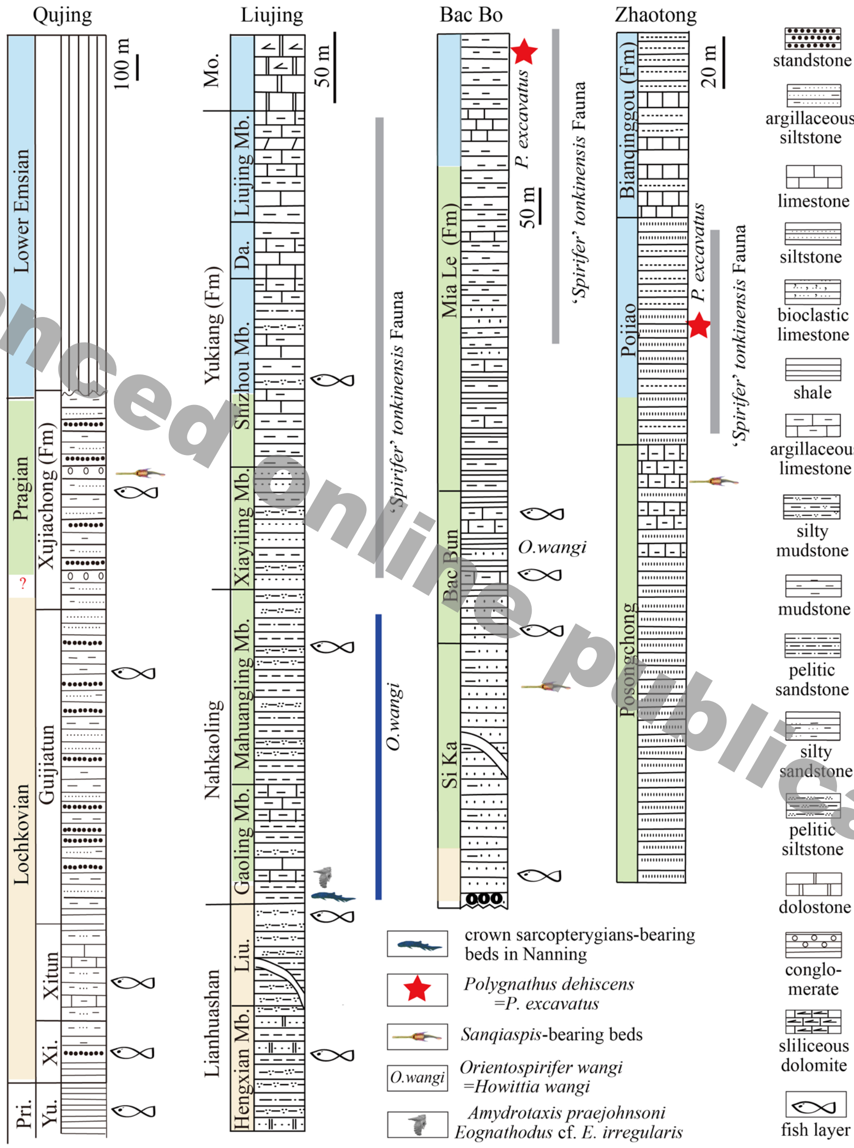

Fig. 7 Dating and correlation of the Early Devonian stratigraphy from four selected section areas in South China Block

Data are from Liao et al., 1978, 1979; Ma et al., 2009; Xue et al., 2018; Guo et al., 2019; Qie et al., 2019; Yu et al., 2020; Gai et al., 2022; Lu et al., 2023

Abbreviations: Da. Daliancun Member; Fm. Formation; Hen. Hengxian Member; Liu. Liukankou Member; Mb. Member; Mo. Moding Formation; Pri. Pridoli; Xi. Xishancun Formation; Yu. Yulungssu Formation

The preservation condition in the Nanning area is similar to the materials in Qujing and northern Vietnam. It should be noted that the fossil assemblages recovered from the Nanning and Qujing areas display significant similarities to each other. However, they are still different in the general faunal composition. For example, large-sized taxa such as *Youngolepis* are more abundant in Nanning, and small to medium-sized taxa are more abundant in Qujing. The faunal composition difference likely results from paleoecological differences, which need further analysis. During the Early Devonian, marine transgression reached central and western parts of Guangxi, including the Liujing and Dale areas. At that time, sea-level changes easily produced frequent lithological changes under a largely nearshore, open, shallow water environment, probably bringing large amounts of food and oxygen.

5 Conclusions

We report four sarcopterygians (*Psarolepis*, *Youngolepis*, *Diabolepis*, and *Styloichthys*) from the Lianhuashan and Nahkaoling formations (Lochkovian, Lower Devonian) of Nanning, Guangxi, which provide new data for the Lower Devonian stratigraphic correlation between southwestern China and northern Vietnam. Based on the conodont evidence and new fossil fish discovery, we propose that the Xujiachong Assemblage has a much longer range than previously supposed, extending from the latest Lochkovian to the end of Pragian, and the transition of the Nahkaoling and Lianhuashan formations in Nanning might correspond to the Guijiatun Formation in Qujing. The large size of fossil fish individuals in Nanning may be related to the increase in oxygen content around that area.

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广西下泥盆统的肉鳍鱼类化石

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摘要：记述了广西南宁下泥盆统莲花山组和那高岭组中发现的早期肉鳍鱼类化石，材料包括一件斑鳞鱼(*Psarolepis*)的左侧颊板骨，一件杨氏鱼(*Youngolepis*)的后顶甲，一件奇异鱼(*Diabolepis*)的颅顶甲和一枚蝶柱鱼(*Styloichthys*)鳞片。其中颊板骨标本代表了目前已知最晚的斑鳞鱼化石记录，奇异鱼和蝶柱鱼标本则是这两个属在云南曲靖以外的首次报道。这些材料丰富了徐家冲组合的生物面貌，为广西、云南和越南北部下泥盆统的地层对比提供了重要化石证据。根据最新的牙形石证据，广西南宁地区的徐家冲组合可能最早在晚洛霍考夫期就已出现，比其他地区该组合的出现时间更早。广西南宁的莲花山组与那高岭组的过渡地层可能与曲靖地区的桂家屯组时代相当。同时，南宁地区的鱼类化石标本较云南曲靖地区的有明显大型化趋势，可能与当时南宁地区鱼类的生活环境中氧含量高有关。

关键词：广西南宁，下泥盆统，洛霍考夫期，徐家冲组合，莲花山组，那高岭组，肉鳍鱼类

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